Catalogue of American Amphibians and Reptiles.

Kaiser, H. and J.D. Hardy, Jr. 1994. *Eleutherodactylus johnstonei.*

Eleutherodactylus johnstonei Barbour
Johnstone's Whistling Frog
Rainette de Johnstone

Eleutherodactylus johnstonei Barbour, 1914:249. Type-locality, "St. Georges, Grenada." Two syntypes, Museum of Comparative Zoology, Harvard University (MCZ) 2759, collected by G.M. Allen and C.T. Brues, exact date of collection unknown (examined by authors).

Hylodes johnstonei: Nieden, 1923:421.

Hyla barbudensis: Auffenberg, 1958:251. Type-locality, "Cave I, Two Foot Bay, Barbuda." Holotype, University of Florida Collections (UF) 2752, a fossil right ilium, collected by W. Auffenberg and W. King on 3 July 1958 (not examined by authors).

Eleutherodactylus barbudensis: Lynch, 1966:524.

Eleutherodactylus johnstonii: Sutherland and Nunnemacher, 1981:415 (see Nomenclatural History).

Eleutherodactylus johnstoni: Gorzula, 1989:56 (see Nomenclatural History).

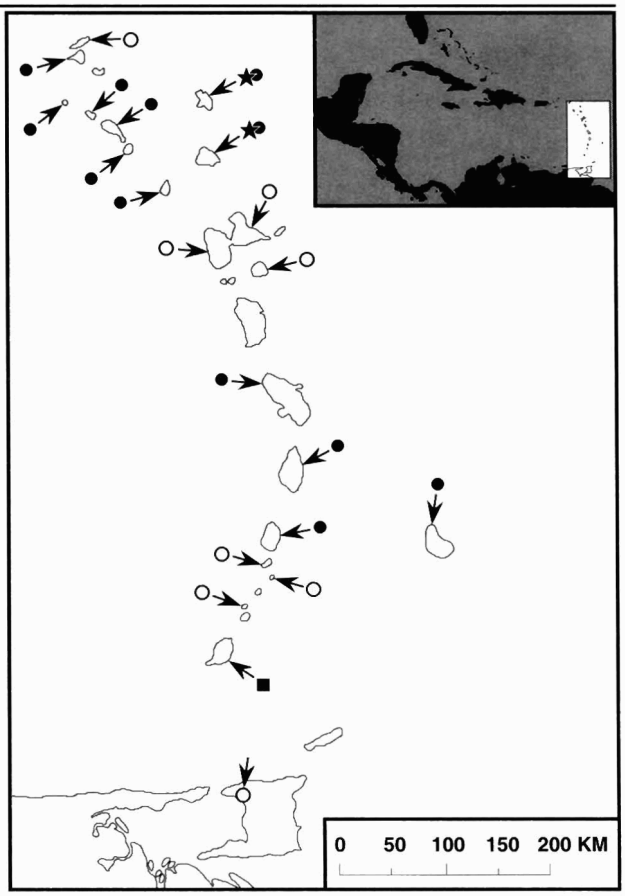
• **Content.** The species is monotypic.

• **Definition.** This species is a medium-sized *Eleutherodactylus* (males and females to 25 and 35 mm SVL, respectively), placed by Schwartz (1967, 1969) into the *E. auriculatus* species group. Dorsal coloration is brown to grayish-brown, with a great variety of dorsal patterns. Most specimens have a scapular chevron, often in combination with one or more other pattern elements, such as a second chevron, a pale median hairline, or prominent pale dorsolateral stripes (Schwartz, 1967). Detailed descriptions of pattern variation were given by Schwartz (1967).

• **Diagnosis.** This species of *Eleutherodactylus* may be distinguished from all other members of the genus by the following characteristics: hind limbs of medium length (tibia $\bar{x}$ = 44.3 ± 3.4% SVL), head of moderate width (head width $\bar{x}$ = 38.9 ± 2.0% SVL), single crural crossbar, hidden surfaces of hindlimbs and groin irregularly patterned, but never colored red. Choanae are small; dentigerous processes of vomers in very small patches, enclosed within inner margins of choanae. Inguinal glands are absent.

• **Descriptions.** Schwartz (1967) enumerated the morphological characteristics of *E. johnstonei*, especially those important in distinguishing it from *E. martinicensis*, as part of a comparative synopsis of all *Eleutherodactylus* from the Lesser Antilles. He included several metric characters to illustrate inter-island differences. Other, less detailed descriptions were provided by Barbour (1914, 1916a), Nieden (1923), Parker (1933), Bayley (1950), Schwartz and Fowler (1973), and Schwartz and Henderson (1991). Joglar (1986, 1989) listed *E. johnstonei* as a member of his *unistrigatus* group and provided a character state list for 52 morphological and life history characters. Hedges (1988, 1989) placed this species into his subgenus *Eleutherodactylus*, *auriculatus* section, *martinicensis* series, *martinicensis* group, together with the other Lesser Antillean species listed by Schwartz (1967). The call of *E. johnstonei*, described by Watkins et al. (1970), Lemon (1971), Hardy and Harris (1979), and Kaiser (1992), consists of two notes. The first note has a mean frequency near 2000 Hz and a duration of 0.07-0.09 s. The second note is longer (duration 0.18-0.27 s) and given in a frequency range of 3300-4100 Hz. The average interval between successive calls is 1.2 s, with a maximum of about 60 calls per minute.

Figure 1. *Eleutherodactylus johnstonei* from Barbados.



Map. The solid square is the island where the type was collected. Dots indicate historic records, circles mark introductions documented in the last fifteen years. Stars indicate fossil localities. Various introductions have established the species in locations well beyond its Lesser Antillean range. Localized populations occur in Guyana (Georgetown), Venezuela (Caracas, Cumaná, Ciudad Bolívar, and some other urban centers), Jamaica, Panamá [City], Curaçao, and Bermuda.

• **Illustrations.** Photographs of *E. johnstonei* are in Pope (1917), Rekum (1961), Lamotte and Lescure (1977), and Beckwith (1986). Series of photographs in Lyons (1979) and Reubold (1983) show various egg clutches, emerging hatchlings, and juvenile frogs. Line drawings of whole animals or appendages were presented by Barbour (1914) and Schwartz (1967). Drawings of the ilium are in Auffenberg (1958) and Lynch (1966). Audiospectrograms of the mating call were published by Watkins et al. (1970), Lemon (1971), Hardy and Harris (1979), and Kaiser (1992). The ontogeny of *E. johnstonei* is illustrated in Peters (1876), Bayley (1950), Adamson et al. (1960), Chibon (1960), Lamotte and Lescure (1977), and Hourdry and Beaumont (1985). A drawing of the egg tooth is in Lamotte and Lescure (1977).

• **Distribution.** *Eleutherodactylus johnstonei* is one of the most widely distributed species of the genus *Eleutherodactylus*; and is present on all major Lesser Antillean islands (with the apparent exception of Dominica), as well as at various localized geographically distant points (see Table). This distribution has been shown to be the

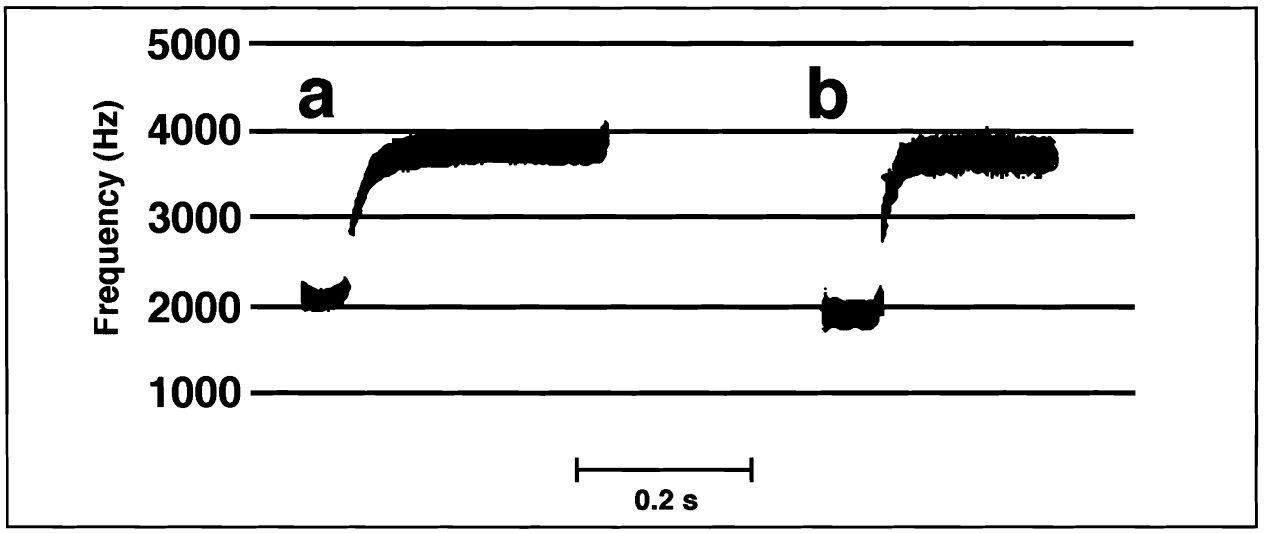


Figure 2. Audiospectrograms of the call of *Eleutherodactylus johnstonei*: (a) Galways Soufriere, Montserrat, 25 August 1990, recorded by H. Kaiser and C.A. George; (b) Grand Etang, Grenada, 1 August 1990, recorded by H. Kaiser and H.H. Schwarten.

result of many introductions, achieved mainly through human agency (Kaiser, 1992).

In his initial species description, Barbour (1914) limited the distribution of *E. johnstonei* to Barbados and Grenada, noting that it was introduced to Grenada from Barbados in about 1885. Barbour (1916b) noted that the existence of the species in the Barbados highlands may indicate a long presence on that island, contrary to the reports of early chroniclers (see also Marsh, 1983). In addition, Schwartz (1967) listed Antigua, Barbuda, Martinique, Montserrat, Nevis, Saba, St. Eustatius, St. Kitts, St. Lucia, St. Martin, and St. Vincent. Hardy (1970) and Hardy and Harris (1979) reported *E. johnstonei* from Guyana (Georgetown), Venezuela (Caracas, Cumaná), and Curaçao. Schwartz et al. (1978) added Guadeloupe to the distribution, a record verified by Hardy (1985) but erroneously restricted to the Basse-Terre portion by Hedges and Thomas (1989). Schwartz and Henderson (1991) listed St. Barthélemy as part of the distribution, but this record apparently refers to the recent introduction of *E. martinicensis* (Kaiser, 1992). Introductions in the late 1800s and in the early part of this century (see Table) took place in Bermuda (Pope, 1917), England (Günther, 1895), Jamaica (Barbour, 1910; Dunn, 1926; Lynn, 1940; Perkins, 1942), and "hot houses in Europe and North America" (Barbour, 1930:77). Undoubtedly, historic distributional records were influenced by the similar morphology of *E. johnstonei* and *E. martinicensis*, a conclusion reflected in the species lists published in the early part of this century (Barbour, 1930, 1935, 1937). We have personally verified the distributions in the Lesser Antilles, Guadeloupe, Guyana (Georgetown), and Venezuela (Caracas). New records of established populations of *E. johnstonei* (see Table) exist for Anguilla (Censky, 1989), several of the Grenadines (Lazell and Sinclair, 1990; Henderson et al., 1992), the Grande-Terre portion of Guadeloupe (Henderson et al., 1992), Marie-Galante (Henderson et al., 1992), Panamá [City] (Ibáñez and Rand, 1990), Trinidad (Kenny, 1980), and several urban areas in Venezuela (Gorzula, 1989).

• **Fossil Record.** Fossil remnants of small frogs from Barbuda referable to *E. johnstonei* are described and figured in Auffenberg (1958) and Lynch (1966). Steadman et al. (1984) and Pregill et al. (1988) listed fossil anuran materials from Burma Quarry, Antigua.

• **Pertinent Literature.** During our literature survey, we realized that the taxonomic confusion of *E. johnstonei* with its

Table. Documented introductions of Johnstone's Whistling Frog, *Eleutherodactylus johnstonei* Barbour. Approximate dates are marked with a dagger (†), questionable origins are marked with an asterisk (*). Dates for apparently unsuccessful introductions are given in parentheses.

Location	Year	Origin	References
Anguilla	between 1982–87	St. Maarten *	Censky (1989)
Barbados [1]	1879 †	?	Fielden (1889), Schwartz (1967)
Bequia	late 1980s	?	Lazell and Sinclair (1990)
Bermuda	1880 (?) and 1886	Jamaica	Pope (1917)
Curaçao	1975 †	?	Hardy and Harris (1979)
Dominica	(1979)	?	Kaiser (1992)
England (London)	1885	?	Günther (1895)
Grenada [1]	1885 †	Barbados	Barbour (1914), Schwartz (1967)
Guadeloupe	1970s	?	Schwartz et al. (1978)
Guyana (Georgetown)	1923 †	Barbados *	Hardy and Harris (1979), Lescure (1983)
Jamaica (Kingston area)	1890	Barbados *	Barbour (1910), Dunn (1926), Perkins (1942)
Marie-Galante	1990	?	Henderson et al. (1992)
Mustique	1990 †	?	Henderson et al. (1992)
Panamá [City]	between 1984–87	Windward Islands	Ibañez and Rand (1990)
Trinidad (Arima Valley)	(1970s)	?	Hardy and Harris (1979)
Trinidad (Port-of-Spain)	1980	?	Kenny (1980)
Union Island	1990 †	?	Henderson et al. (1992)
Venezuela (Caracas)	1958 †	?	Hardy and Harris (1979)
Venezuela (Cumaná)	1967	Caracas	Hardy and Harris (1979)
Venezuela (various urban areas)	1960s–1980s	Caracas *	Gorzula (1989)

[1] The accuracy of the timing for introductions to Barbados and Grenada is still in doubt (Schwartz, 1967). In general, travel reports and anectodal evidence from the 17th and 18th centuries, the primary sources for faunal distribution records on these islands, will also reflect the difficulties faced by the authors in accessing remote areas of the islands. Consequently, omissions in faunal lists may not be uncommon, particularly with respect to nocturnal species (Marsh, 1983).

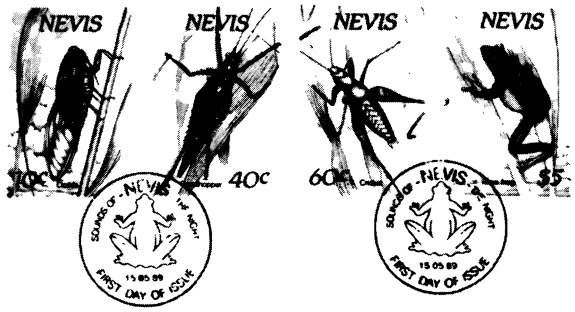


Figure 3. Series of stamps issued by Nevis celebrating the "Sounds of the Night." A likeness of *Eleutherodactylus johnstonei* carried the highest denomination and also was accorded special importance by serving as a symbol on the cancellation for first day-of-issue covers.

presumed close relative *E. martinicensis* (Kaiser, 1993; Kaiser et al., 1994) is very wide-spread. We therefore have assured by careful study of the texts and by locality data that the literature listed below refers only to *E. johnstonei*, even though the actual citation may indicate otherwise.

The most comprehensive work on the morphology of *E. johnstonei* is the synopsis by Schwartz (1967). A shorter description and a brief account of the natural history can be found in Schwartz and Henderson (1991). Development was described by Peters (1876), Bayley (1950), Adamson et al. (1960), Chibon (1960, 1962), and Lamotte and Lescure (1977). The figures from Peters' (1876) description of direct development were frequently used in textbook accounts of animal development for over 40 years (e.g., Knauer, 1878; Kingsley, 1885; Boettger and Pechuel-Loesche, 1892; Gadow, 1901; Boulenger, 1910). Chibon (1962) reported that female *E. johnstonei* are able to breed about every two to three months throughout the year under laboratory conditions, becoming mature at under one year after hatching. Long (1974), Lamotte and Lescure (1977), and Hardy (1984) described the egg tooth. Goin (1959) reported the average number of maxillary teeth as 80 (N = 14). Lescure (1980) provided a brief account of clutch attendance with descriptions of eggs, egg clutches, and egg deposition sites. Hardy and Harris (1979) and Hardy (1985) compared leg muscle proteins of several Lesser Antillean species, and Hardy (1985) reported a chromosome number of 2n = 28. Allozyme polymorphisms were used by Kaiser et al. (1994) to develop systematic and biogeographic hypotheses for *E. johnstonei* and other Eastern Caribbean *Eleutherodactylus*. Stewart (1977) and Stewart and Martin (1980) reported on the use of coconut husk-piles as daytime refugia and egg deposition sites, and on a population removal-reinvasion experiment. Bayley (1950), Ovaska (1991a, b, 1992), and Ovaska and Hunte (1992) studied various aspects of the ecology and behavior of *E. johnstonei* on Barbados, with Lescure (1966) providing brief information from Martinique. An overview of the importance of this species to conservation issues in the Lesser Antilles was provided by Kaiser and Henderson (1994). Heatwole and Newby (1972) provided data on the relationship between body moisture content and activity levels. Pough et al. (1977) investigated heat and drying tolerance, water loss, and temperature selection. Hughes (1962, 1964a, b, c, 1965a, b, c, d, 1966a) and Hughes and Egar (1972) conducted limb transplantation experiments with *E. johnstonei* embryos. Experiments on the development of the nervous system were performed by Lynn and Peadon (1955) and Hughes (1966b). Spinal nerve fiber sizes and counts were made by Sutherland and Nunnemacher (1981). Jaeger and Hailman (1976) investigated phototaxis, and Millott and Lynn (1954) conducted experiments on pigmentation. Welsh and Zipf (1966) estimated the amount of 5-hydroxytryptamine in the skin of *E. johnstonei*, and Burnie (1989) and Everard et al. (1990) investigated parasitism. A discussion of the *M. depressor mandibulae* was presented by Lynch (1993).

• **Nomenclatural History.** Several attempts have been made to clarify the nomenclatural history of *E. johnstonei* (Schwartz, 1967; Wingate, 1969; Schwartz and Thomas, 1975; Frost, 1985), yet despite these efforts some confusion remains. The exact timing of the initial collections of *Eleutherodactylus* in the West Indies is not known, but presumably, French collectors integrated some specimens into the Paris collections near the end of the eighteenth century. Tschudi (1838:37) involuntarily created a *nomen nudum* when explaining his find of "*Hyla martinicensis*" in the Paris collections; but, in the same publication, he (Tschudi, 1838:77) aligned the species with *Hylodes* without further comment. Duméril and Bibron (1841) then synonymized their manuscript name *Eleutherodactylus* with Tschudi's species (but see Myers, 1962, for a more complete taxonomic history of the generic nomenclature). Since then, Lesser Antillean *Eleutherodactylus* were called *E. martinicensis* until Barbour (1914) described *E. johnstonei*. However, even that species designation did not succeed in clarifying the taxonomic identities of *E. johnstonei* and *E. martinicensis*, as is apparent from several post-Barbour publications (Nieden, 1923; Parker, 1933; Dunn, 1934; Goin and Cooper, 1950; Lynn, 1957; Grant, 1959; Adamson et al., 1960; Hughes, 1962; Lemon, 1971). The correct interpretation of species designations from that time therefore is difficult if locality data are imprecise or unavailable. The fossil described by Auffenberg (1958) as *Hyla barbudensis* and later referred to *E. barbudensis* by Lynch (1966) was synonymized with *E. johnstonei* by Pregill et al. (1988). The uses of the names *E. johnstonii* by Sutherland and Nunnemacher (1981) and *E. johnstoni* by Gorzula (1989) are unjustified emendations, probably caused by misspelling.

• **Remarks.** Several authors have suggested that transport of *E. johnstonei* likely occurred with plant or vegetable matter (Barbour, 1930; Goin, 1944; Censky, 1989; Kaiser, 1992) and that colonization was then facilitated by man-made irrigation schemes (Barbour, 1930; Censky, 1989; Kaiser, 1992). On Bermuda, *E. johnstonei* was introduced later than *E. gossei* (Pope, 1917), which may have impeded its invasion (Wingate, 1965). However, by 1964, *E. johnstonei* had become the more abundant species on Bermuda, possibly due to its superior colonizing abilities (Wingate, 1965; Pough et al., 1977; Stewart, 1977; Hardy and Harris, 1979; Stewart and Martin, 1980).

• **Etymology.** Barbour (1914) named the species for Robert S. Johnstone, at that time Chief Justice of Grenada and the Grenadines, for his aid to the collectors.

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